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Liverpool Marine Biology Committee.

L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY W. A. HERDMAN, D.Sc., F.R.S.

V.

ALCYONIUM

BY

SYDNEY J. HICKSON, M.A., D.Sc., F.R.S.,

Beyer Professor of Zoology in the Owens College, Manchester

(With 3 Plates)

PRICE EIGHTEENPENCE.

LONDON
WILLIAMS & NORGATE
JANUARY, 1901.

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ALCYONIUM

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EDITOR'S PREFACE.

The Liverpool Marine Biology Committee was constituted in 1886, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Fourteen Annual Reports of the Committee and five volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the sea-shore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and convenient Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man.

In these thirteen years' experience of a Biological Station (five years at Puffin Island and eight at Port Erin), where College students and young amateurs formed a large proportion of the workers, the want has been constantly felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many College laboratories.

The objects of the Committee and of the workers at the Biological Station have hitherto been chiefly faunistic and speciographic. The work must necessarily be so at first

when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits: but the majority of the papers in the volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Committee hope in the future to add greatly to the records of the Fauna and Flora. But the papers in the present series are quite distinct from these previous publications in name, in treatment, and in purpose. They will be called the "L.M.B.C. Memoirs," each will treat of one type, and they will be issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear, or later bound up in convenient volumes. It is hoped that such a series of special-studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

It is proposed that the forms selected should, as far as possible, be common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. Probably most of the specialists who have taken part in the L.M.B.C. work in the past, will prepare accounts of one or more representatives of their groups. The following have already promised their services, and in many cases the Memoir is already far advanced. The first Memoir appeared in October and the second in December, 1899, the third in February, and the fourth in April, 1900, this fifth one will be issued about the end of

1900, and the sixth will be ready early in 1901 ; others will follow, it is hoped, in rapid succession.

Memoir I. Ascidia, W. A. Herdman, 60 pp., 5 Pls., 2s.
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Buccinum, M. F. Woodward.
Calcareous Sponge, R. Hanitsch.
Arenicola, J. H. Ashworth.
Antedon, H. C. Chadwick.
Oyster, W. A. Herdman and J. T. Jenkins.
Porpoise, A. M. Paterson.

In addition to these, other Memoirs will be arranged

for, on suitable types, such as *Sagitta* (by Mr. Cole), a Cestode and a Turbellarian (by Mr. Shipley), *Carcinus*, an Amphipod, and a Pycnogonid (probably by Dr. A. R. Jackson).

As announced in the preface to Ascidia, a donation from Mr. F. H. Gossage of Woolton met the expense of preparing the plates in illustration of the first few Memoirs, and so enabled the Committee to commence the publication of the series sooner than would otherwise have been possible. A second donation received since from Mr. Gossage, and another recently from Mrs. Holt, are regarded by the Committee as a welcome encouragement, and will be a great help in carrying on the work.

W. A. Herdman.

University College, Liverpool,
December, 1900.

L.M.B.C. MEMOIRS.

No. V. ALCYONIUM.

BY

SYDNEY J. HICKSON, M.A., D.Sc., F.R.S.

Introduction.

The Order Alcyonaria is represented in the British seas by very few species; and as none of these are commonly found between tide marks nor thrown up on the beach by storms, they are very little known to the general public. The Alcyonarian which is best known to the public is the precious coral of commerce, *Corallium rubrum*, from the Mediterranean Sea, but other Alcyonarians, such as the Organ pipe coral (*Tubipora*), the Blue coral (*Heliopora*), the Sea-fans (Gorgonacea) and the Sea-pens (Pennatulacea) are familiar objects in our Zoological Museums.

When a living Alcyonarian is examined in sea-water a number of tubular radially symmetrical bodies are seen to project from the surface, each of which is provided at its free extremity with eight pinnate tentacles arranged in a circle round a slit-like mouth. When the water is disturbed, or the Alcyonarian removed from the water, these bodies slowly retract beneath the surface of the coral, until their presence is indicated only by an eight-rayed star-like aperture. These bodies are usually called

the polyps, and they undoubtedly possess many features of general resemblance to the well-known fresh-water polyp Hydra. A critical examination of the anatomical structure of the Alcyonarian, however, proves that the name "polyp" is misapplied in this case, for the bodies referred to only correspond with a part of the polyp of the Hydra, namely, the free end with the crown of tentacles, the greater part of the fixed or proximal end of the Alcyonarian polyp being buried in the massive substance of the coral. We have, in other words, two parts in the body of the Alcyonarian polyp,—(i.) a part which is free and can be retracted or expanded at will, and (ii.) a part which is attached and firmly welded to the corresponding parts of neighbouring polyps.

With this explanation of the general structure the reader is prepared to understand the critical or diagnostic features by which a given specimen may or may not be referred to the Order Alcyonaria.

The Alcyonaria are Coelenterata which (with one or two rare exceptions) form colonial organisations by budding. The individual polyps composing the colony are provided with eight tentacles at their free extremity, and each of these tentacles is provided with two or more rows of papilliform processes called pinnules, giving the tentacles a feathered or pinnate form.

The form which the Alcyonarian colony takes varies immensely in the different families into which the Order is divided: some being encrusting plates, some lobular in form, some shrubby, some mushroom shaped, and so on, but a detailed description of these forms would take me beyond the scope of this memoir. The important point to note here, however, is that although there is a remarkable

similarity in the form of the polyps of any one species, the shape of the colony has wide limits of possible variation, and consequently a definition of it is almost impossible.

In other respects, too, the species vary. The colour, for example, is sometimes constant, but more generally subject to considerable variation, and the spicules, which are often very characteristic in form, more frequently are subject to modification in size and form from that which is regarded as typical of the species.

The reproduction of the Alcyonarians is remarkably constant. A few species are viviparous, the young being born as solid, oval, ciliated larvæ, which swim away and then settle down to found a new colony. In the majority of cases, however, the eggs and sperms are discharged into the water simultaneously by the male and female colonies, fertilisation is effected in the water, and solid oval embryos are produced similar to those of the viviparous species. No other larval form is known in the group, and nothing occurs in the development of any species of the nature of an alternation of generations.

With the exception of the Precious Coral, the axis of which is used by jewellers, none of the Alcyonarians have any market value. Nor do the Alcyonarians, so far as we know at present, form an important article of food for fish or indeed any other marine animals. It is true that occasionally fragments of Pennatulids are found in the stomachs of Codfish, but there is no reason to believe that they form a frequent nor a favourite diet.* It is possible that at the spawning period of the Alcyonarians many of the eggs and embryos are devoured, but of this there is at present no definite evidence.

* The Haddock is sometimes found with pieces of the Pennatulid *Virgularia* in its stomach. *Vide* A. M. & W. F. Marshall, Report on the Oban Pennatulida, Birmingham, 1882.

Alcyonium digitatum.

This species has a very wide distribution in the British area, and may be regarded as one of the most abundant of British marine animals, as it appears to be capable of adapting itself to a very great range of natural conditions; but although so common, it is not found in many places at low tides. It is found in great numbers growing on the shells of Pectens, Cardiums, and other Mollusca on sandy, gravelly or shelly trawling grounds. It occurs attached to rocks which are exposed at low tides, and even on iron pillars of piers just below low-water mark, and encrusting worm tubes on muddy bottoms. Its vertical range extends from shallow water to a depth of 383 fathoms ("Caudan"), but probably depths of 35-40 fathoms, *i.e.*, the usual limit of wave action (as Allen has pointed out) are most suitable for its maximum growth and development. Geographically it extends from the coast of Norway (Hardanger fjord) to the Bay of Biscay, and it seems probable that there is no considerable extent of the British area which is free from it. I am indebted to Mr. Chadwick for the following notes as to the distribution of *Alcyonium digitatum* in the L.M.B.C. district. "Very small colonies are sometimes found at extreme low-water mark in Port Erin Bay, and large ones, of both colour varieties, occur in large numbers on the blocks of concrete forming the now ruined breakwater. We occasionally dredge colonies from depths of 12 to 15 fathoms in this neighbourhood. I have seen several very fine ones brought up on the long lines used by our fishermen. The greatest depth of which we have a record is 21 fathoms, on North Bank, 7 miles W. of Peel. It is pretty generally distributed all round the Manx coast. *Alcyonium* used to be abundant and the colonies of large size on some reefs

of sandstone exposed only at the lowest tides at Hilbre Island. It is still to be found there, but in diminishing quantity, owing to the increase of sewage and chemical refuse in the river Dee. Small colonies occur rarely at extreme low water mark on the beach at Beaumaris, and large ones may be found at the same level in the caves on the N. side of Puffin Island. I have dredged well-grown colonies from depths varying from 5 to 10 fathoms in the Menai Straits. Red Wharf Bay, Anglesey, depth 4 to 7 fathoms, is another Welsh locality."* An account of the distribution of *Alcyonium* in the Plymouth district is given by Mr. E. J. Allen in the Journal of the Marine Biological Association, Vol. V., No. 4, 1899.

The size of the colony varies from that of a small pin's head to six inches or more in height by eight inches in breadth, according to the age of the colony and the number of polyps of which it is composed. The shape also varies very considerably. In the Plymouth district I found the smallest forms to be flat encrusting plates, which soon become convex above, and then grow into dome-shaped and later spherical lumps, and similar stages are found at Port Erin and elsewhere. Until the colony reaches a height of 3 inches from the support on which it grows it is not branched, but the larger specimens are divided terminally into 2, 3, 4, 5 or 6 blunt lobes which have a very rough resemblance to large human toes (Plate I., figs. 1 and 2). As these lobes are nearly always arranged in one plane the popular name of "Dead men's toes" has been applied to the species.

The method of growth of the colony which is given here is not constant; but no systematic investigation has yet been made of the laws which govern the growth of this

* See also Herdman, L.M.B.C. Report No. I, 1886, on the Alcyonaria of L.M.B.C. district.

and other genera belonging to the Alcyonaria. The colonies which grow on worm tubes seem to require a broader base than the others, and several specimens have been obtained which appear to be mainly encrusting plates, the vertical growth being relatively very slight. The specimens which grow on rocks, on the other hand, usually exhibit a much narrower base of support, grow rapidly in height and branch earlier and more freely than others.

The colour is usually pale flesh-colour when the colony is fresh, but this soon fades in an aquarium, and the colony becomes white. Many freshly-caught colonies from Plymouth Harbour were quite pale when brought into the laboratory, but perhaps their conditions of life were not perfectly healthy. A yellow variety of several tints is frequently found. I have obtained specimens of it from the West Coast of Scotland, Port Erin, Puffin Island, the Bristol Channel and elsewhere. This colour is due to a fixed pigment in the spicules, and it shows no appreciable change after years of immersion in spirit. At Port Erin there are two distinct tints of the yellow variety recognised, the one paler and the other a deep orange. I do not think that a red colour in the spicules ever occurs in this species. The red Alcyonium discovered by Couch off the coast of Scotland is *Alcyonium glomeratum* of Hassall, and is distinct from *A. digitatum*, Linn, in various respects.

Reproduction.

Alcyonium digitatum is always dioecious. No hermaphrodite colonies have yet been observed. The eggs, when ripe, are of a yellowish-red colour, and are discharged into the water by the mouths of the polyps which bear them. At the same time of the year

the ripe sperm sacs of the males which are always milky white in colour, and can therefore be readily distinguished from the ova, discharge great quantities of spermatozoa into the body cavity, and thence by way of the mouth into the water. Fertilisation is most probably effected in the water, and not in the body cavity of the female just before the discharge of the ova. If this is the case, the sexual act is a true process of spawning.

The exact time of spawning may vary in different localities. In the Plymouth district I have found, as a result of a six years' series of observations, that the spawning always occurs during the last fortnight in December and the first fortnight in January, and at no other time of the year. At Port Erin the spawning may be somewhat later, as I have examined larvæ captured with the Plankton at Easter, which I feel certain are the larvæ of *Alcyonium digitatum*.

Anatomy of the Colony.

When a colony of *Alcyonium* is cut across (Plate I., fig. 5) it will be seen to consist mainly of a number of parallel tubes perforating a semi-transparent gelatinous substance in which a number of small calcareous spicules are imbedded. Each of these tubes is the body cavity—or coelenteron - of a polyp, and the gelatinous substance is the mesogloea of the polyps fused together into a common mass.

When the colony is alive and in a healthy condition a number of delicate transparent polyp heads protrude from the surface of the colony. Each of these is provided with a mouth and eight pinnate tentacles, and the body-wall below the crown of tentacles encloses a single large cavity, which is continuous with the cavity of the tubes

above-mentioned. A careful examination of the body-wall of the polyp heads with a microscope (Pl. II., fig. 15) reveals the fact that it consists of three layers, an outer layer of cells—the ectoderm, a middle homogeneous layer —the mesogloea and an inner layer of cells—the endoderm. If these three layers be traced down to the surface of the colony it will be found that the ectoderm is continued over the general surface of the colony as a covering or protective sheath, that the mesogloea is continuous with the gelatinous mass or mesogloea common to the individuals composing the colony, and that the endoderm forms an inner lining to the tubes almost to the base of the colony.

The colony then is formed of a number of individuals, each of which consists of two parts—a greater part below bound to its neighbours in a common mesogloea, and a smaller part above which is free.

This latter part can be introverted into the former for protection—in much the same way as the head of the tortoise can be withdrawn into the shelter of the carapace —and it may be distinguished by the name "anthocodia" suggested by Mr. Bourne. When the "anthocodia" is retracted the aperture of the tube or false mouth can be constricted and closed so as to give complete protection to the polyp, as seen by reference to Plate I., fig. 3, in which a series of stages of the retraction of the anthocodiæ is illustrated. This power which the colony possesses of completely closing the "false mouths" of the polyps is of some physiological interest, as it enables each polyp of the colony to retain in its cavity a sufficient supply of sea-water to maintain its vitality for a few hours when the tide is exceptionally low and the colony is exposed to the air. Without this power the delicate cells which cover the tentacles and body-wall of

the anthocodiæ would be very quickly killed when the colony is taken from the sea. As it is, colonies of *Alcyonium* will retain their vitality for two or three days if packed in damp seaweed.

The number of the polyps in each colony increases with its age, young buds being formed between the older polyps all through the life of the colony. Each of these buds is formed from an outgrowth of one of the superficial canals (which may be seen to ramify in the mesogloea near the surface of colony—Pl. I., fig. 3) joining a corresponding depression from the ectoderm at the surface. The young polyps thus formed remain in communication with the neighbouring older polyps by the canal throughout life, but no new canalicular communications with these older polyps are formed at a later period excepting quite close to the surface. The connection, therefore, between the polyps composing the colony is that represented in Plate I. fig. 5. The cavities of the older polyps are here seen to extend to the base of the piece that is represented in section, the cavities of the younger polyps are connected at their bases with them by short canals, and these in their turn may be connected with the bases of still younger polyps in a similar manner.

The colonial mesogloea appears to be at first sight a homogeneous substance, but an examination with a simple magnifying lens shows that it bears, firstly, a number of small white calcareous bodies called "the spicules," secondly, the canals above-mentioned, and, thirdly, a number of very fine branching lines which might be mistaken for capillary tubes.

(i.) The spicules are small bodies varying in size according to their age, but when fully formed 0·1-0·3mm. in length. They are composed of calcium carbonate with a sparse organic matrix. They vary very considerably in

shape belonging to the categories which specialists call "warted spindles" (Pl. III., fig. 21), dumb-bells (fig. 22), Ks (fig. 23), and simple crosses. They are formed in cells budded off from the superficial ectoderm, and are only newly formed at the surface. This accounts for the fact that they are always much more crowded at the surface than they are in the more deep-seated parts of the colony, and also for the fact that in the deeper parts the spicules are always of full size.

(ii.) The canals are seen most clearly near the surface of the colony (Plate I., fig. 3). They have a sinuous course and appear to anastomose freely. They probably serve the purposes of distributing nourishment and of maintaining an equilibrium in the water pressure of the polyp cavities.

(iii.) The fine lines, which look like capillary tubes, really consist of strings or rows of cells. They have no lumen, and consequently cannot serve the purpose of transmitting the circulating fluids of the body. We have no definite knowledge of their function, but it is probable that they are mainly concerned in the secretion of the mesogloea.

Anatomy of the Polyps.

The structure of the anthocodiæ can only be satisfactorily studied when they are fully expanded. When retracted the several organs are so tightly compressed that a correct interpretation of their structure is quite impossible. When fully expanded each anthocodia exhibits a terminal slit-shaped mouth (Pl. I., fig. 4) surrounded by a crown of eight tentacles. The tentacles have a row of short papilliform processes on each side, giving them what is called a pinnate form. The shape of the tentacles changes every moment, slowly extending and retracting or bending inwards and outwards as they are stimulated by minute particles floating in the water. In the living

condition the tentacles and body wall of the anthocodiæ are very transparent, and many features of the anatomy can be seen without dissection.*

The details of anatomy that can be seen in a living anthocodia are as follows:—From the mouth there hangs down into the body cavity a short opaque throat—the stomodæum (*St.*)—which opens freely below. At this—the lower—aperture six short sinuous cords, the mesenterial filaments, arise attached to the free edges of six very thin vertical plates—the mesenteries (conf. Pl. I., fig. 4, Pl. II., fig. 15, *Mst.*)—and, in addition, there are two cords which pass straight down into the cavity of the polyp attached to the free edges of the two remaining mesenteries. These two straight cords are called the dorsal mesenterial filaments, and the mesenteries which support them the dorsal mesenteries. The other mesenteries are called the dorso-laterals, ventro-laterals and ventrals respectively.

Further details can only be studied in preparations made for microscopic examination.

Nematocysts.—The pinnules of the tentacles bear a number of very minute stinging organs—the nematocysts. They are extremely small (0·0075mm. in length), and may be easily overlooked. They are oval in shape, and when irritated discharge a plain unarmed thread (Pl. II., figs. 8, 9, 10 and 11). Each nematocyst is formed within a specialised ectodermal cell called the "enidoblast."

The Stomodæum is lined internally by a columnar ciliated epithelium, usually thrown into a number of folds in the preparation. On one side there is a groove lined by specialised epithelium armed with relatively long

* The transparency varies in specimens from different localities. In some cases there are so many spicules in the anthocodia that the transparency is very considerably diminished. The figure 4 in Plate I. was drawn from a Plymouth specimen.

powerful cilia. This groove is the siphonoglyph (Pl. II., fig. 6). The siphonoglyph indicates the position of the ventral side of the polyp.

The Mesenteries.—The mesenteries are in the greater part of their course very thin, consisting of two layers of endoderm cells covering a thin sheet of mesogloea. In the region of the stomodæum, however, they exhibit longitudinal thickenings or ridges which support the muscular fibres that are principally concerned in the retraction of the anthocodia. The arrangement of these thickenings is very characteristic. They are all situated on the ventral faces of the mesenteries, so that in a transverse section the muscle ridges on the ventral mesenteries are face to face, and on the dorsal mesenteries they are back to back (Plate II., fig. 6).

In the last six months of the year all the mesenteries, with the exception of the two dorsals, bear a considerable number of spherical bodies which are ova or sperm sacs according to the sex of the colony (Plate III., fig. 20).

The two dorsal mesenterial filaments run straight down from the lower end of the stomodæum into the depths of the polyp cavities. In the cavities of the older polyps they may be traced almost to the base of the colony. The epithelium covering these filaments is columnar and ciliated, the cilia producing in life a current of water flowing towards the stomodæum. The other mesenterial filaments are of a perfectly different nature (Pl. II., fig. 15). They are much shorter than the dorsal filaments, and are covered by an epithelium densely packed with gland cells. Their function is to secrete a digestive juice upon particles of food which pass through the stomodæum.

The Endoderm lining the cœlenteric cavity in the anthocodia is composed of ciliated cubical cells closely packed to form an epithelium. In the lower parts of the

tube the cells are not so tightly packed, and each one bears at its base a process containing a myophan thread (Pl. II., fig. 12). These threads are so arranged as to form a circular muscle band by the constriction of which the diameter of the tube may be diminished.

It is a perfectly easy operation to scrape away on to a glass slide a number of the endodermal myo-epithelial cells in *Alcyonium*, and mount them for microscopic examination. As a matter of fact they afford us the most readily accessible example of this kind of cell which can be procured.

The Nervous System of *Alcyonium* can only be demonstrated in sections that have been specially prepared. It consists of a few minute star-like cells situated in the mesogloea close to the endoderm and ectoderm layers of the polyps, connected together by very fine anastomosing nerve fibrils.

Mesogloea.—The substance of the mesogloea is, according to Brown, chiefly composed of a Hyalogen. Previous to the conversion of the Hyalogen into Hyalin it yields a Mucin. It does not contain Gelatine, and consequently to speak of it as a gelatinous structure is liable to misinterpretation.

Sexual Organs.—In the month of April several mesenteries bear close to their free borders little groups of cells derived from the endoderm. These cells give rise to the sexual cells, and at this stage the sexes cannot be distinguished. Later in the year the groups of cells become differentiated. In the females the protoplasm of the cells composing a group fuses into a common mass, the nuclei diminish in number, and at length there remains only one large spherical cell with one nucleus (See Pl. III., fig. 19). This cell is a young ovum. It grows very slowly in size, and spherical globules of some

kind of fatty food material which we may call yolk, appear in its cell substance. The only other changes that take place during the last six months of the year are the appearance of a yellowish red pigment at the periphery and, in the last month, the transit of the large nucleus to one side of the ovum (Plate II., fig. 13). In the males the group of primary sexual cells that are formed on the mesenteries in the spring undergo rapid cell division, and a spermary is thus formed, packed with very minute cells. The protoplasm of these cells is so tightly pressed together that the spermary has the appearance of being a single cell, with an enormous number of nuclei. When the spermary is about 0·1 mm. in diameter, the cells collect towards the periphery, leaving a rounded space containing strands and lumps of protoplasm (Plate II., fig. 14). This central body may correspond with the "blastophore," which occurs in the spermatogenesis of some other animals. The ripe spermatozoa which are only found in December completely fill the cavity of the spermary. They consist of a head with a cone-shaped anterior end, followed by a spherical body, and a long flexible tail.

Development.

When the ova are ripe, they are about 0·5 mm. in diameter, and they are discharged into the water by way of the mouth the stomodaeum distending considerably to allow them to pass. If we may judge from what may be seen in an aquarium, the spawning is a very lengthy process, as each ovum takes at least ten minutes to pass through the stomodaeum. At any rate, they do not appear to be "vomited forth in great masses," as they are in *Renilla*, according to Wilson.

The early stages of development are probably very variable as regards the external signs of segmentation.

It is certainly the case, however, that some young embryos which appear to be unsegmented when examined whole with a simple lens are found, in sections, to be more advanced than others which are clearly segmented. It is really quite impossible to say, in the present state of our knowledge, what is the "normal" or "typical" proceeding at this early stage. There is a stage, however, occurring a few hours after fertilisation, in which the embryo consists of a single mass of protoplasm containing several protoplasmic "islands" almost free from yolk in each of which there is a nucleus (Pl. III., fig. 16). It is really a "morula" stage, although it may or may not exhibit mulberry markings externally. The "islands" of protoplasm and their nuclei increase rapidly in number, and soon the outlines marking the boundaries of the cells become clearly differentiated. The nucleus of the cells in these stages divides by a well-defined karyokinesis (fig. 17), several beautiful achromatic spindles with their chromosomes being seen in sections of every well-preserved embryo that is examined. A cavity makes its appearance in the interior of the mass of cells constituting the embryo and at the same time the cells at the circumference become arranged in a definite row.

In the next stage (fig. 18) a definite ectoderm is formed at the periphery. This layer differs from the layer of embryonal cells of the last stage in the fact that it is clear and devoid of yolk globules and that the cells are ciliated. Inside the ectoderm there is still a layer of undifferentiated embryonal tissue, laden with yolk, enclosing an irregular cavity.

Later stages than this of the larval development have not yet been discovered, and it is not known how the stomodæum and mesenteries are formed. It is probable, however, that soon after the mouth is formed the larva

settles down on a rock or shell at the bottom, loses its cilia and assumes the characters of a single Alcyonarian polyp. The youngest stage that the author has seen after fixation is shown on Plate III., fig. 24. In this case the primary polyp has already formed one secondary polyp by gemmation.

Physiology.

When the polyps of an *Alcyonium* are fully expanded they are in a state of physiological activity, the muscles are constantly contracting, the cilia vibrating, and other functions of the body being performed. This functional activity does not go on continuously, but at times the anthocodiæ are all retracted, and a period of rest supervenes. There can be little doubt that the period of rest occurs rhythmically, the rhythm corresponding not with the light and darkness of day and night, but with the high and low tides. As a result of some experiments that were made a few years ago, it seems probable that *Alcyonium* rests regularly at every low tide, that is to say, twice in every day and night, but owing to the unsatisfactory conditions appertaining to life in a sea-water aquarium, it is not possible to state how long the periods of rest last in natural healthy surroundings.

Circulation.—It is certain that in such a fleshy mass as a colony of *Alcyonium* presents, a free circulation of a liquid throughout the whole system is absolutely necessary for the respiration of the tissues. In the absence of any rhythmically contractile organ which could be called a heart, how is this circulation maintained? The answer is, entirely by ciliary action. When the polyps are expanded, a current of water is produced by the constant vibration of the long cilia of the siphonoglyph, which flows from the mouth downwards into the coelenteric cavities. It is probable that some of the fresh sea-water

thus inhaled is driven by vortices created by the cilia of the endoderm into the canals of the mesogloea, and thus the rapidly growing parts of the colony are supplied with oxygenated water. The remainder travels down the ventral sides of the coelenteric cavities. A current of water in the opposite direction is produced by the cilia of the long dorsal mesenterial filaments (see Plate III., fig. 20 *Dmf.*) which probably makes its exit by way of the dorsal side of the stomodaeum. In this manner a regular circulation of the water in the colony is maintained during the time when the polyps are expanded.

Digestion.—Particles of food which are caught by the tentacles are, if suitable in size, passed to the mouth and rapidly swallowed by the stomodaeum. The stomodaeum in *Alcyonium* is not, as it is in *Xenia*, and some other Alcyonarians, a digestive tube. The food is unaltered during its passage through it. On passing the lower or inner opening of the stomodaeum the six ventral mesenterial filaments embrace it, and hold it fast for some time. During this time the glands on these mesenterial filaments secrete a digestive fluid, which partly dissolves it and breaks it up. The food which is thus dissolved is assimilated by the general endoderm lining the coelenteron, and possibly also by the ventral mesenterial filaments themselves. Food particles that escape from the embrace of the mesenterial filaments and particles of oil or fat which are not dissolved by the digestive ferment are swallowed by endoderm cells and digested intracellularly. The ferment of the digestive fluid secreted by the filaments is alkaline in most Coelenterates, and the ferment secreted by the endoderm cells into their food vacuoles is an acid ferment. From the few observations that have been made on *Alcyonium*, it is probable that in this respect it agrees with other Anthozoa.

The above description of the anatomy and development of *Alcyonium digitatum* is compiled entirely from my own observations. A considerable part of the work has already been published in a paper which appeared in the Quarterly Journal of Microscopical Science. Volume 37, and the reader may be referred to this for further information on the histology of the species. The account of the chemistry of the mesogloea was published in the same volume by Mr. Brown.

An important paper has recently been published by Mr. G. C. Bourne in the "Transactions of the Linnæan Society," Vol. VII., pt. 10, on the genus *Lemnalia*, in which the term "Anthocodia," which has been adopted in this memoir, and others which will be useful to students of the Alcyonaria are introduced for the first time.

Explanation of the Plates.

Plate I.

Fig. 1. A small specimen of *Alcyonium digitatum*, L., natural size, killed in such a manner that some of the anthocodiæ (*i.e.*, polyp-heads) have remained expanded while the others are completely or wholly retracted. The anthocodiæ on the knob seen at the right hand side of the drawing, for example, are retracted, and the star-like depressions indicating their positions are the "false mouths," as explained in the text. This figure is drawn from a specimen taken at Port Erin.

Fig. 2. Another specimen of *Alcyonium digitatum* drawn in outline and reduced about $\frac{1}{3}$ diam. to show the blunt lobe-like processes that are

frequently formed in the older colonies. This figure is drawn from a specimen in the Cambridge Museum.

Fig. 3. Vertical section through a portion of a colony (semi-diagrammatic) to show the anthocodia in different stages of retraction, the different sizes of the polyps, the general arrangement of the canal system, the position of the spicules, &c. The mesenterial filaments are represented as being in the same plane as the tentacles, which they are not, in order to illustrate certain points in their relations. The following points are illustrated in this figure: 1′ represents the fully-expanded anthocodia of a polyp, 2′ represents a partially retracted anthocodia in which the tentacles are contracted and folded inwards towards the mouth, the body-wall forms a circular fold over the crown of tentacles, 3′ represents an anthocodia in which the tentacles and stomodaeum have sunk to the level of the general surface of the colony, 4′ an anthocodia which has sunk below the surface, and 5′ an anthocodia completely retracted, the false mouth having closed. It will be noticed that the long (dorsal) mesenterial filaments are represented as being all on the left side of the polyps. This indicates that the axis of the lobe from which the section was made was on the left side of the drawing.

Fig. 4. A fully-expanded anthocodia drawn from a living specimen at Plymouth. The bases of the tentacles are extended in a bullate

fashion, and the pinnules are somewhat contracted. The stomodaeum (*St.*) and the six short and two long mesenterial filaments may be seen through the transparent body-wall. At the base of the crown of tentacles, and at the region where the anthocodia abuts on the general surface of the colony the body-wall is rather more opaque owing to the presence of several spicules.

Fig. 5. A diagram of a section through a portion of a lobe, to show the mode of communication between the polyp cavities in the inner parts of the colony.

Plate II.

Fig. 6. Transverse section through an expanded anthocodia in the region of the stomodaeum, showing the siphonoglyph (*Si.*), the folded epithelium on the rest of the stomodaeum (*St.*) the arrangement of the retractor muscles (*Msc.*) on the mesenteries, and the structure of the body-wall. *Ect.* = Ectoderm. *Mes.* = Mesogloea, and *End.* = Endoderm.

Fig. 7. A series of stages of the final development of the spermatozoa as seen in a preparation made by breaking open a spermary in December. *a.* a ripe spermatozoon, *b. c. d.* and *e* stages in the formation of the tail, *f.* a cell with four nuclei occasionally met with in these preparations.

Fig. 8. A cnidoblast, containing an immature nematocyst.

Fig. 9. A mature nematocyst.

Figs. 10 and 11. Two nematocysts after their discharge.

Fig. 12. Two endodermal myo-epithelial cells.

Fig. 13. Section through an ovum early in December, showing the large germinal vesicle close to the periphery and the single large germinal spot which it contains.

Fig. 14. Section through a spermary in the autumn, showing the endodermal capsule which covers it, the central (*bl.*) protoplasmic mass (blastophor) in the centre, and the densely crowded nuclei in the periphery.

Fig. 15. Diagrammatic vertical section through an anthocodia. *Si.* the siphonoglyph on the ventral side of the stomodaeum. *Vmf.* a ventral mesenterial filament. *Mst.* a ventral mesentery. *R.Msc.* retractor muscle. *T.* tentacle. *Gon.* Gonad, and the other letterings as in Fig. 6.

Plate III.

Figs. 16, 17, 18. Three stages in the development of *Alcyonium*, as seen in transverse section. Fig. 16, the morula stage of eight cells, the nuclei of three of these cells can be seen in a star-shaped island of clear protoplasm, the remainder of each cell is filled with closely crowded globules of yolk, which are not represented in the drawing. Fig. 17. A later stage in which a space has appeared in the centre of the embryo, but the cells are still undifferentiated. Fig. 18. A planula stage, in which the archenteric space is much larger, the ectoderm is fully differentiated and ciliated, and the endoderm a continuous

nucleated syncytium undifferentiated into endoderm cells.

Fig. 19. A section through a ventral mesentery in the summer, showing the manner in which ova are formed. *a*. A clump of endoderm cells sinking below the surface. *b*. A nest of young egg-mother cells. *c*. A stage in which the protoplasm of the cells composing a nest has fused into a single mass, and the number of nuclei is reduced considerably. *d*. Last stage in which only one nucleus, the germinal vesicle of the ovum, remains and the ovum has begun to increase in size. The retractor muscles *R. Msc.* of the mesentery are here seen in transverse section.

Fig. 20. Transverse section of an anthocodia in the region of the gonads, showing the six mesenteries bearing ova and the two (dorsal) mesenteries which are barren, *Dmf*.

Figs. 21, 22, 23. Three types of spicules met with in *Alcyonium*.

Fig. 24. The youngest stage of colony formation that has been found by the author.

C. Tinling & Co., Printers, 53, Victoria Street, Liverpool.

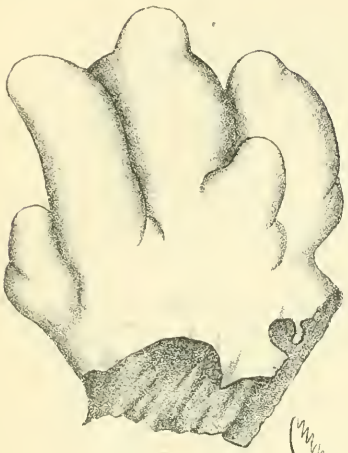
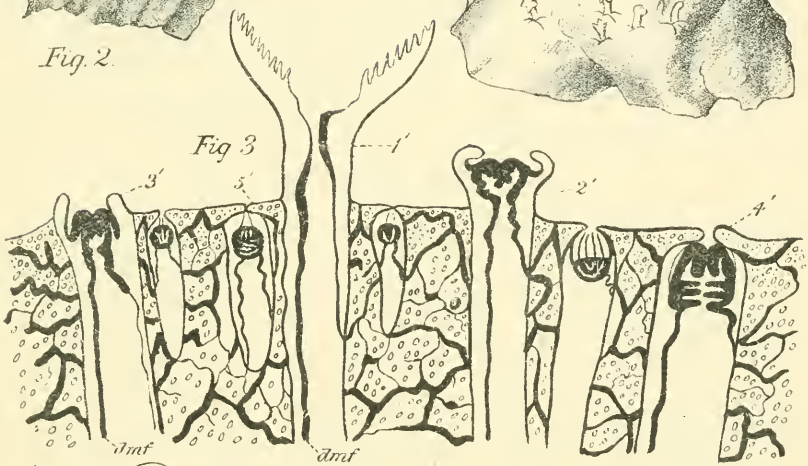
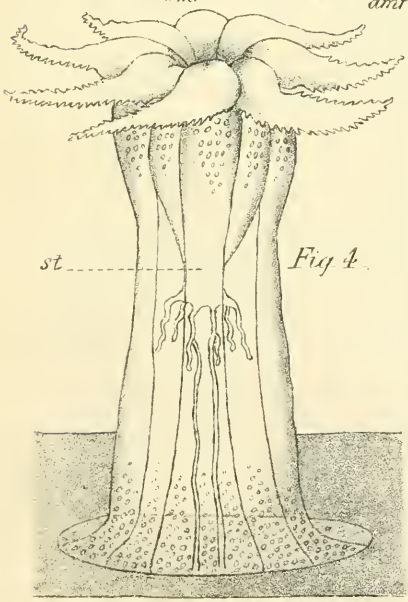


Fig. 2.

Fig. 1

Fig 3





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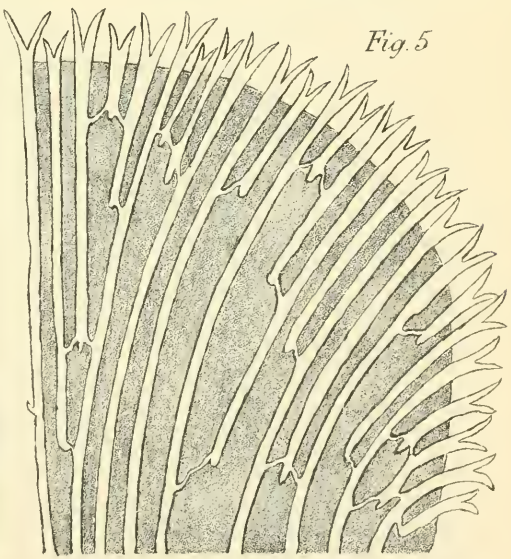
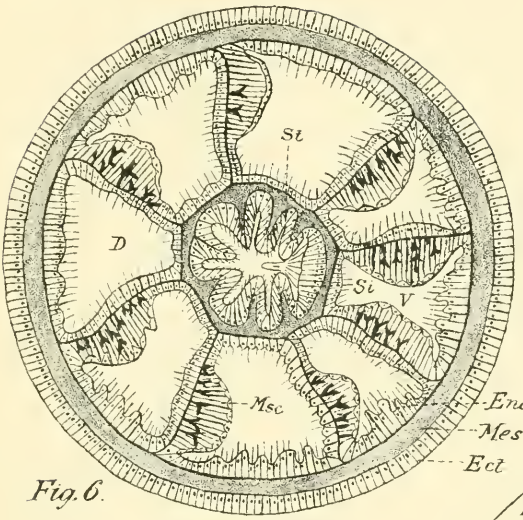


Fig. 5

D. & S. J. H. del.

S. B. lith

ALCYONIUM.



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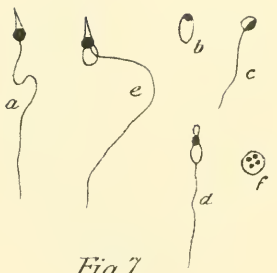


Fig. 7.

Fig. 10

Fig. 11.

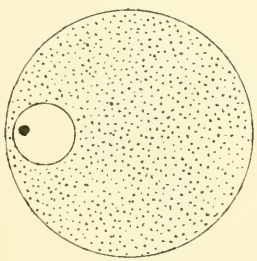


Fig. 13

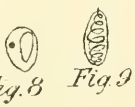


Fig. 8 Fig. 9

Fig 12

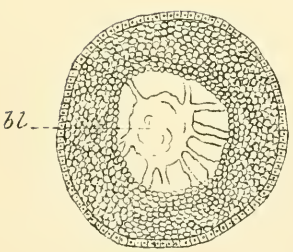


Fig 14

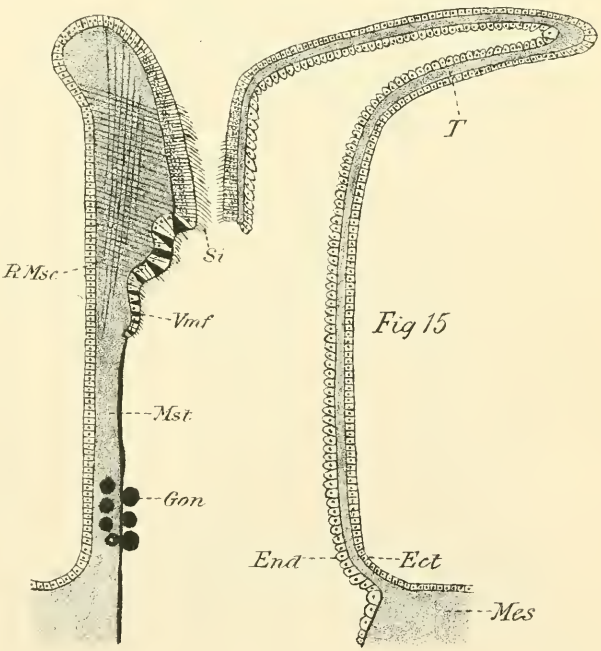
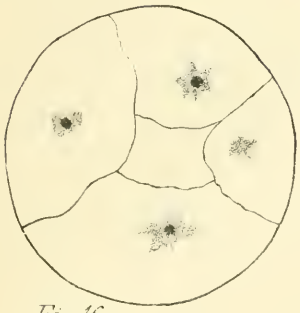


Fig 15

& S. J. H. del.

S. B lith

ALCYONIUM.



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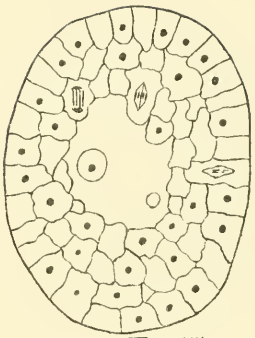

Fig. 17

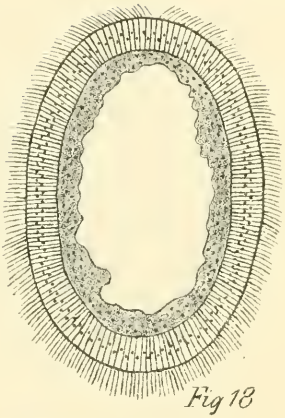

Fig. 18

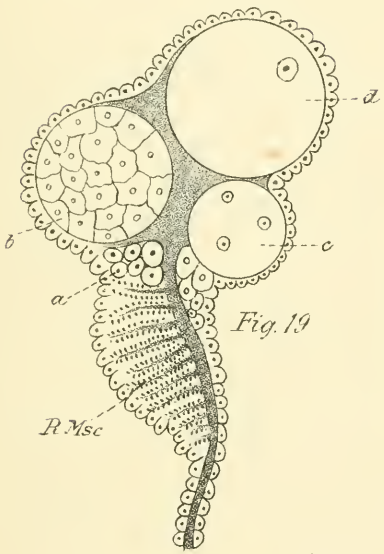

Fig. 19

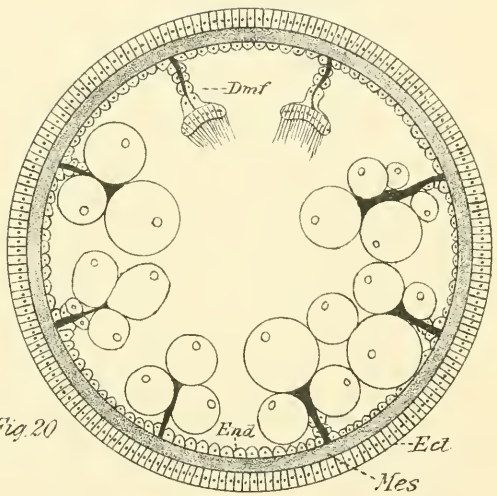

Fig. 20

Fig. 21

Fig. 22

Fig. 23

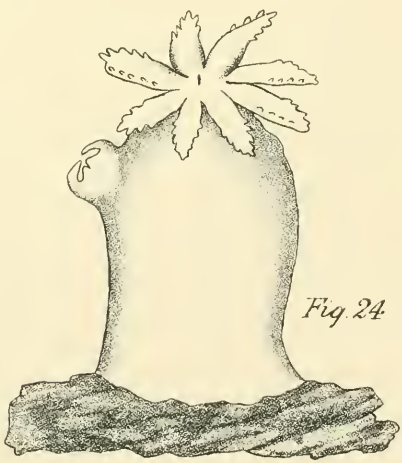

Fig. 24

S. J. H. del.

S. B. lith.

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